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Global analysis of depletion and recovery of seabed biota following bottom trawling disturbance

Running title: Effects of bottom trawling on seabed biota

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27

28 **Statement of authorship:** All authors contributed to data-collation. RH, MJK and SJ initiated the
29 study. JGH and SJ developed the analysis and modelling framework. JGH analysed data. JGH, MJK
30 and SJ wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

31

32 **Data accessibility statement:** All data supporting the results is available in the SI appendix.

33

34 **Keywords:** beam trawl, benthic invertebrate communities, impacts, meta-analysis, logistic recovery
35 model, otter trawl, penetration depth, scallop dredge, systematic review

Abstract

Bottom trawling is the most widespread human activity affecting seabed habitats. Here, we collate all available data for experimental and comparative studies of trawling impacts on whole communities of seabed macro-invertebrates on sedimentary habitats and develop novel and widely applicable methods to estimate depletion and recovery rates of biota following trawling. Depletion of biota and trawl penetration into the seabed are highly correlated. Otter trawls caused the least depletion, removing 6% of biota per pass and penetrating the seabed on average down to 2.4cm, while hydraulic dredges caused the most depletion, removing 41% of biota and penetrating the seabed on average 16.1cm. Median recovery times post-trawling (from 50% to 95% of unimpacted biomass) ranged between 1.9 and 6.4y. By accounting for the effects of penetration depth, environmental variation and uncertainty, the models explained much of the variability of depletion and recovery estimates from single studies. Coupled with large-scale, high-resolution maps of trawling frequency and habitat, our estimates of depletion and recovery rates enable the assessment of trawling impacts on unprecedented spatial scales.

51

52 **Significance statement**

53 Bottom trawling is the most widespread source of physical disturbance to the world's seabed.

54 Predictions of trawling impacts are needed to underpin risk assessment, and are relevant for the

55 fishing industry, conservation, management and certification bodies. We estimate depletion and

56 recovery of seabed biota after trawling, by fitting novel models to data from a new global data

57 compilation. Trawl gears removed 6% to 41% of faunal biomass per pass and recovery times post-

58 trawling were 1.9 to 6.4 y depending on fisheries and environmental context. These results allow the

59 estimation of trawling impacts on unprecedented spatial scales and for data poor fisheries, and

60 enables an objective analysis of trade-offs between harvesting fish and the wider ecosystem effects

61 of such activities.

/body

INTRODUCTION

Fisheries using bottom trawls are the most widespread source of anthropogenic physical disturbance to global seabed habitats (1, 2). Almost one quarter of global seafood landings from 2011–2013 were caught by bottom trawls (3). Development of fisheries, conservation and ecosystem-based management strategies requires assessments of the distribution and impact of bottom trawling and the relative status of benthic biota and habitats. There are many drivers for such assessments including (i) policy commitments to an ecosystem approach to fisheries, (ii) requirements to take account of trawling impacts in fisheries and environmental management plans, (iii) demands from certification bodies to assess fisheries' environmental impacts and (iv) the need to evaluate the effects of alternate management measures to meet conservation and management objectives (4, 5, 6). These assessments are used to assess the sustainability of bottom trawl fisheries and formulate priorities for habitat protection and ultimately to achieve a balance between fisheries production and environmental protection. The distribution of bottom trawling is increasingly well characterised by vessel tracking and other monitoring systems (7), but impacts depend on the magnitude of trawling-induced mortality and recovery rates of biota, for which the current evidence base is incomplete, dispersed and often contested (4, 8).

Bottom trawls, (here defined as any towed bottom fishing gear, including otter trawls, beam trawls, scallop dredges and hydraulic dredges) are used to catch fish, crustaceans and bivalves living in, on, or above the seabed (9). Bottom trawling resuspends sediments (10, 11), reduces topographic complexity and biogenic structures (12, 13, 14), reduces faunal biomass, numbers and diversity (15, 16), selects for communities dominated by fauna with faster life histories (17) and produces energy

86 subsidies in the form of carrion (18). These effects lead to changes in community production, trophic
87 structure and function (19, 20). Given the patchy and dynamic distribution of bottom fishing (21),
88 fished seabeds comprise a mosaic of undisturbed, recently impacted and recovering benthic
89 communities and habitats (22). The state of each patch within this mosaic depends on the history
90 and frequency of past trawling impacts and the recovery rates of the biota present (23).

91
92 Recovery rates following trawling depend on recruitment of new individuals, growth of surviving
93 biota and active immigration from adjacent habitat. Most existing estimates of recovery rates come
94 from experimental studies, with changes in abundance recorded before and after experimental
95 trawling (15, 16). While these experiments provide reliable estimates of immediate mortality, their
96 small scale is likely to underestimate recovery time, in particular for mobile fauna. This is because
97 immigration makes a greater contribution to recovery when biota are relatively more abundant
98 around the impacted site, and because most experiments have been conducted in infrequently and
99 untrawled areas (16). On fishing grounds, impacts occur on larger scales such that untrawled and
100 infrequently trawled areas become scarce when there is more trawling activity. Furthermore,
101 experiments typically focus on recovery following single trawling events, rather than recovery from
102 successive events typical of fishing grounds.

103
104 The development of satellite-based vessel monitoring systems has enabled scientists to map
105 commercial fishing activity at high resolution (7). Such maps have been used to design studies of the
106 comparative impacts of towed bottom-fishing gears across gradients of commercial fishing
107 frequency (herein = comparative studies). In contrast to experimental studies, these studies account
108 for the spatial extent, frequency and temporal variability in fishing activity, and are expected to
109 provide more representative estimates of recovery rates. When these estimates are coupled with
110 estimates of the mortality of biota from experimental studies, they can be used to assess status of

impacted biota on fishing grounds. Presently there are too few studies to adopt the alternative approach of analysing large-scale studies directly recording recovery from trawling (24).

We used the logistic growth equation (25) to describe recovery of benthic fauna because it provides an effective abstraction of the complex recovery dynamics of populations and communities and can be fitted to available data (e.g. 26, 23, 22). This model is identical to the Schaefer models commonly used in fisheries management when the data to implement full age or size-structured models are not available (27). If we assume the recovery of biomass or numbers (hereafter abundance) of biota B following trawling is described by the logistic growth equation, then the equilibrium solution can be used to estimate B as a fraction of carrying capacity K in an environment subject to chronic fishing disturbance (28):

$$B/K = 1 - F d/r \quad (\text{eq. 1})$$

where F is trawling frequency, d is the depletion of biota caused by each trawl pass (expressed as a proportion) and r is rate of increase, interpreted here as the recovery rate. Equation (1) only requires estimates of F , d and r to estimate relative abundance B/K (28). Eq. 1 suggests that r is constant, but in communities composed of species with a range of r values, trawling selects for species with faster life histories that are more resilient and therefore r can be expected to increase with F . We found that the relationship between community B/K and F for communities is well approximated by a log-linear relationship (SI appendix, Text S3). We therefore estimated r at $F = 0$ and assuming a log-linear relationship between B/K and F (eq. 2). More sophisticated models of recovery can account for differential responses of groups with contrasting life histories and other aspects of community dynamics, and thus provide a better description of underlying processes (19, 29), but higher parameter demands limit their application to systems with a substantial amount of available data. Conversely, if d and r can be estimated and associated uncertainties quantified, the logistic model would facilitate assessment of trawling impacts in most marine systems. Different

gears and substrata will have different levels of seabed contact or penetration and these factors will influence d . Penetration depth is however largely independent of the towing speed (6). If a strong relationship exists between the penetration depth and d , this can be used to obtain estimates of depletion for trawl gears for which no empirical depletion estimates are available. Trawling frequency F is defined as the swept area ratio, which is the area trawled annually divided by the studied area ($\text{km}^2 \text{ km}^{-2} \text{ y}^{-1}$, simplified to y^{-1}), which should ideally be calculated for small cells (ca. 1km^2) because trawling tends to be spatially clustered at larger scales.

Here, we conduct a meta-analysis of experimental studies of trawling impacts to estimate depletion of biota following trawling. We report the effect on the abundance of whole benthic macro-invertebrates communities, including infauna and epifauna. We combine this with the first meta-analysis of results from large-scale comparative studies of trawling effects on fishing grounds, to estimate recovery rates of seabed biota, and describe how they vary with gear characteristics and environment. All data were collated from studies that were quality assured following systematic review methodology, thereby avoiding selection bias (30).

RESULTS

Twenty-four comparative and 46 experimental studies met the criteria for inclusion in our analyses (SI Appendix, Table S1-S3). Studies were mostly temperate and concentrated in NW Europe and NE USA (Figure 1). None of the studies that met the criteria examined the effect of trawling on biogenic habitats, but there were sufficient studies in other habitats. Many gear-habitat combinations were not represented in the studies reviewed because many fishing gears are only suitable for fishing on particular seabed types or species associated with those habitats (SI Appendix, Table S1) and because some habitats are less widespread than others (7).

160

161 Depletion rates estimated from the experimental studies for biomass and numbers were not
162 significantly different. Thus the pooled estimates of d (SI Appendix, Table S4) apply to both biomass
163 and numbers. Estimates of depletion d and penetration depth P by gear-type were very closely
164 correlated (Figure 2, Pearson's $r = 0.980$, $p = 0.020$). Otter trawls (OT) had the smallest impact,
165 removing on average 6% of organisms per trawl pass and penetrating on average 2.4cm into the
166 sediment. Median penetration depths were 2.7cm and 5.5cm for beam trawls (BT) and toothed
167 dredges (TD) respectively and the corresponding median depletions per trawl pass were 14% and
168 20%. Hydraulic dredges (HD) had the largest impact, removing on average 41% of organisms per pass
169 and penetrating 16.1cm.

170

171 The effect of trawling frequency on relative biomass estimated from the comparative studies
172 showed a log-linear relationship and with each unit increase in swept-area ratio linked to a mean fall
173 in biomass of 15.5% (Figure 3a). None of the other environmental variables significantly affected this
174 response (Table 1). The effect of sediment composition on community biomass depletion was not
175 significant (Table 1A, SI Appendix, Table S5) but the model estimates for gravel are nevertheless
176 shown in the Table 1a to allow comparison with the significant effects of gravel found for community
177 numbers (Table 1B, SI Appendix, Table S5). Mean community r (estimated using equation S4.1 and
178 S4.2 from d and b) increased with trawling frequency, from 0.82 y^{-1} when there was no trawling (5-
179 95% uncertainty intervals $0.42 - 1.53$) to $1.73 (0.89 - 3.23) \text{ y}^{-1}$ when the trawling frequency was 10
180 y^{-1} (using the mean estimated d across gears OT, BT and TD, $d = 0.13$, SI Appendix, Figure S1, Table
181 S6). The increase in r , which results from changes in community composition to favour biota with
182 faster life histories, is therefore relatively slight across ranges of trawling frequencies that dominate
183 those on real fishing grounds, e.g. 0 to 1 y^{-1} (e.g. 31, 7, 32). The r estimate of 0.82 y^{-1} enables
184 estimates of median time to recovery (T) to $0.95K$ for a range of levels of depletion (Figure 3b). For

example, if the fraction depleted $D = 0.5K$ then recovery time is 3.6 years (5-95% uncertainty intervals: 1.9 - 6.4 years).

The effect of trawling on community numbers, estimated from the comparative studies, increased significantly with the gravel content of the sediment (Figure 3c, Table 1B, SI Appendix, Table S5) and this effect persisted when examined among gears. The reduction in benthic community numbers for each unit increase in trawling frequency was 3.1% at 0% gravel content (typical for BT studies), 5.5% at 1% gravel content (typical for OT studies), and 72% at 45% gravel content (typical for TD studies). The estimates of r for community abundance range from 0.18 y^{-1} for TD on 45% gravel to 4.47 y^{-1} for BT on 0% gravel, with high uncertainty. These r estimates result in a median recovery time T from $0.5K$ to $0.95K$ of 0.7 to 16.6 y (Figure 3d). Beside gravel content, the inclusion of the ratio of d over primary production also resulted in reduced AIC compared to the model with no additional explanatory variables, with the effect of trawling on numbers increasing with d and decreasing at higher levels of primary production (Table 1B, SI Appendix, Table S5).

DISCUSSION

This is the first attempt to quantify the impacts of bottom trawling and recovery of seabed biota by synthesizing data from trawling studies following a systematic review of the available evidence-base. We developed a novel method to derive the recovery rates of benthic macrofaunal invertebrate communities from trawling by combining results from experimental and comparative studies, and provide new estimates of depletion and recovery including a quantification of uncertainty based on all available data. The method for estimating the recovery rate from comparative studies is novel. Given that realistic and robust r estimates have been largely unavailable previously, this work is critically important. Recovery rates were estimated from changes in the biomass and numbers of biota across fishing grounds, so estimates are likely applicable to trawled shelf-seas in general (at least in temperate waters where most of the studies were carried out). Our new estimates of

depletion and recovery enable the parameterisation of models to predict the state of the benthic biota as a function of trawling frequency and levels of primary production and % gravel (28). Coupled with the emergence of large-scale estimates of trawling frequency (7) these models will support assessment of trawling impacts on unprecedented spatial scales, because our approach provides a quantitative estimate of status with minimal data requirements (28). The method is widely applicable because it requires relatively few data inputs and could be applied world-wide, including fisheries where trawl impacts remain unassessed. The r and d values that we estimate here with a broad geographic basis are based on the full body of available evidence and are therefore the most robust estimates available. The generality of our approach means that the outputs of assessments are accurate when averaging over larger scales, but that biases may exist when used for local assessments. These results have global policy relevance for conservation and food security policy development as it enables an objective analysis of the efficacy of different methods of harvesting food from the ocean to be considered in the light of the wider ecosystem effects of such activities on the marine environment. The results enable managers to understand the variable resilience of benthic systems to trawl fisheries and to set limits of fishing accordingly.

Most continental shelves consist of relatively small intensively trawled areas where the trawling frequency is in the range of 1 to 10 y^{-1} and extensive infrequently trawled areas where the trawling frequency is $<1 \text{ y}^{-1}$ and predominantly $<0.25 \text{ y}^{-1}$ (7). Our results show that trawling frequencies of 1 y^{-1} cause average declines of 15.5% in the biomass of benthic biota. Communities on gravel may be more sensitive to trawling because they on average have a larger proportion of larger, long-lived and sessile epifauna (33) that are particularly sensitive to trawling (34). Effects were greater for gears that kill a larger fraction of the biota (larger d) because they penetrate the sediment more deeply, and weaker in areas of higher primary production where higher food supply to the benthos may result in a higher recovery rate.

235

236 The ranking of different fishing gears with respect to their magnitude of impact reported here is
237 similar to the ranking in previous meta-analyses of small-scale experimental studies (15, 16),
238 although our estimates of d are smaller, probably because we adjusted for the number of trawl
239 passes while previous analyses did not. The use of depletion to primary production ratio as a proxy
240 for community resilience to trawling has the advantage of being easily understandable and easy to
241 estimate for new areas and fisheries. The ratio of depletion over primary production might support
242 rapid preliminary large-scale risk assessments of potential trawling impacts on community
243 abundance to guide more region-specific studies. The close relationship between penetration depth
244 and depletion can be used to estimate depletion resulting from the pass of a given trawl gear when
245 no direct depletion estimate is available. Accurate estimates of penetration depth are much easier
246 and cheaper to obtain than estimates of depletion, would support preliminary impact assessments
247 by gear type, and can even be generated using numerical models (11).

248

249 Our analyses did not identify any variables other than trawling frequency that affected community
250 biomass. This is surprising given the contrasting results for numbers and that some comparative
251 studies and past meta-analyses of experimental studies have shown interaction effects between
252 gear type and habitat type (e.g. 29, 16). The relatively small number of studies included in the
253 biomass analysis and the high variability associated with benthic sampling, which cannot be fully
254 controlled in a meta-analysis, may have contributed to this discrepancy. Our results for biomass
255 imply that a single estimate of recovery rate r is appropriate when assessing impacts on the different
256 habitat types studied here. They also suggest that differences in time to recovery and expected
257 biomass (B/K) will be driven primarily by gear type (and hence d) and trawling frequency (F).

258

Our estimates of biomass recovery times are similar to empirical measurements of recovery taken in three areas where commercial trawling was stopped (4-5 years, 24), but are longer than estimates from small-scale experimental studies, which are in the order of 25–500 days (15, 16). The scale-dependency of recovery times has important implications for management because recovery will be faster when trawled areas are closer to less impacted areas from which individuals can recruit or migrate (as also shown by 22). We found that biomass recovery rates were slower and recovery times longer than those for numbers. This result is expected based on the population dynamics of seabed biota. Recovery in numbers is driven more strongly by recruitment than recovery of biomass, which is driven by increases in the size and age structure of the population through growth of individuals. We recommend the use of recovery rates for community biomass when modelling trawl impacts and their consequences. This will give due weight to recovery of body-size and age structure as well as numbers and take account of energy flow through food webs and other ecosystem processes that are linked closely to biomass. Recovery times as estimated from the logistic model nevertheless do not imply that the communities will recover over these times to the species, size and age composition that existed before trawling, but they do imply the recovery of total biomass or numbers and related cross-species ecosystem processes such as aggregate secondary production.

Uncertainties around mean/median estimates of penetration depth, recovery and depletion were high, despite the careful screening of included data (but which also decreased the sample size and potentially power to detect effects, 30). However, our approach allows us to address directly some aspects of uncertainty, and the broad distribution of resulting depletion and recovery estimates show that large site-specific differences in the response of seabed communities to trawling are expected. The advantage of characterising uncertainty is that it can be propagated in future risk and impact analyses. Given the unexplained variance in r , percentiles from the distribution of plausible values might be selected to reflect the degree of risk aversion in the management system. The

284 extent of risk aversion is a non-scientific decision (although it would be informed by science) that
285 would likely be made by managers and other stakeholders. Risk aversion would likely depend on the
286 perceived value of a habitat type. A risk-averse approach might adopt a value of r from a lower
287 percentile of the distribution (e.g. the 10% or 25%) rather than the median (see SI Appendix, Table
288 S6 for a selection of values).

289
290 Our use of comparative studies provides improved estimates of recovery compared with those from
291 previous small-scale experiments studies because they are based on larger scale measurements
292 from fishing grounds. Comparative studies may however be affected by ‘shifting baselines’ (35),
293 where historical trawling has removed the most sensitive organisms and only resilient organisms
294 remain. Since trawling selects for species with faster life histories that are more resilient, recovery
295 time will increase with trawling frequency. Our finding that mean community r increases with F
296 conforms with previous observations of shifts towards species with faster life-histories in disturbed
297 communities (e.g. 36). This effect is apparent across a range of plausible trawling frequencies from
298 >0 to 10 y^{-1} but would be small for the great proportion of most fishing grounds where swept area
299 ratio is less than 1 y^{-1} (7). Although this shift means that previously trawled communities may be
300 more resilient to further trawling, it does not mean that they will recover any faster to the original,
301 pre-trawling state. For this reason we used the r estimate of untrawled communities for estimating
302 recovery times. Selective effects linked to trawling history are likely to be strongest for long-lived
303 sessile epifauna that build biogenic reefs, such as sponges and corals. The estimates of r and T
304 presented here are applicable to invertebrate communities living in sedimentary habitats, but not
305 biogenic habitats as no studies of trawling impacts on biogenic habitats met the rigorous selection
306 criteria imposed by the systematic review.

In summary, we apply novel and widely applicable methods to estimate depletion and recovery rates of benthic invertebrate communities following trawling. By accounting for the effects of gear type and penetration, environmental variation and uncertainty, our analysis explained much of the variability of depletion and recovery estimates from single studies. Coupled with large-scale, high-resolution maps of trawling frequency and habitat, our estimates of depletion and recovery rates will enable analysis of trawling impacts on unprecedented spatial scales to inform best-practices to achieve sustainable fishing, and will be of use to policy makers, conservation planners and fisheries managers for risk assessment and the evaluation of management strategies.

METHODS

We present analyses for whole community biomass and numbers of benthic invertebrates. Changes in the abundance of seabed biota following trawling depend on the mortality caused by each pass of a trawl and the rate of recovery of the biota between trawl passes. We estimated the immediate depletion of biota (d) caused by a trawl pass from a meta-analysis of experimental studies of trawling impacts. We estimated the recovery rates (r) of biota from a meta-analysis of comparative studies of trawling impacts. The analyses were structured to assess the effects of gear type, penetration depth and environmental variables (e.g. depth, sediment composition) on depletion and recovery.

Depletion

Depletion was estimated using data collated from experimental studies of trawling impacts identified using systematic review methodology. A comprehensive literature search of journal papers, book chapters and grey literature reports was carried out. Details of literature search terms and databases, study inclusion criteria are provided in the systematic review protocol by Hughes et

al. (30). All included studies quantified the immediate mortality of biota following one or multiple trawling events. Each identified study had to pass quality assurance criteria before data from the study were included in the collated dataset.

We classified gear types as otter trawls, beam trawls, towed dredges or hydraulic dredges (SI Appendix, Text S1). The reduction in abundance of biota resulting from one pass of a trawling gear depends on the characteristics and operation mode of the gear. Different gears are designed to have different levels of seabed contact or penetration, depending on the target species and seabed type, and these factors will influence mortality (37). Consequently, we assessed the relationship between mortality and penetration depth of the gear. Some of these studies were conducted in previously trawled areas with a lowered abundance of biota, but as we are estimating the fraction of organisms removed rather than the absolute amount we expect that this will have had little effect on our estimates of d . Depletion d was estimated using a generalized linear mixed model (GLMM) implemented in the package *nlme* in R (38, 39), with $\ln RR$ (the log of the ratio of the biomass or abundance in trawled over untrawled areas) as the response variable, and \log_2 (time t in days since trawling) and gear type as fixed factors, and the study as a random effect assuming a Gaussian error distribution. We weighted $\ln RR$ values by the inverse of their variance as is normal practice in meta-analyses. We estimated d as the intercept for the different gears at $t = 0$.

Predicted penetration depth of each gear type into the seabed was estimated from values in the literature by averaging the reported penetration depths of the individual components of the gear (e.g. doors, sweeps, and bridles of an OT) weighted by the width of these components (details in SI Appendix, Text S2).

Recovery

Recovery rates were estimated using data collated from comparative studies of trawling impacts. All included studies sampled the biomass or numbers of whole communities of benthic invertebrates at two or more sites subject to different trawling intensities on commercial fishing grounds. Contributing studies were identified following the same procedure as for experimental studies (SI Appendix, Text S1). In the analyses of the comparative studies we assume that both K and observed gradients of trawling effort were unrelated to other environmental drivers, and that the observed state of the biota is in equilibrium with the reported trawling effort. Gradients in trawling effort may be driven by regulation and seabed obstructions, but are also observed in areas of homogenous habitat (e.g. 29). Spatial patterns of trawling effort are also shown to be relatively stable over time in the few fisheries where high-resolution time series have been analyzed (40). K could vary across the trawl grounds because of environmental variations and this will increase the uncertainty around relationships between B and F .

In the comparative studies, conversions between units of abundance were not always possible (e.g. biomass per unit sediment volume could not be converted to biomass per unit sediment area, given sampling gears with different, but unknown, efficiencies), so absolute B or K could not be estimated. We normalized the data by expressing relative biomass or numbers as the B/K ratio and used a log-linear approximation for the relationship between community B/K and F where

$$\log_{10}(B/K) \sim b F \quad (\text{eq. 2})$$

where b is the slope of the relationship (derivation taking account of the log-linear relationship between B/K and F and the distribution of trawling in SI Appendix, Text S3 and S4). After fitting a linear relationship to $\log_{10} B$ versus F for each comparative study, K was estimated as the $10^{\text{intercept}}$ of this relationship.

380

381 The data collated from comparative studies were initially used to estimate relative changes in
382 abundance (B/K) as a function of trawling frequency F . This approach differs from the
383 aforementioned analyses of depletion because the change in abundance with trawling is a response
384 to both depletion (per trawl pass) and recovery. Because $b = d/r$ (equation 1), once d is estimated
385 from experimental data, recovery rate r can be estimated from the slope b of equation (2) after
386 taking account of the log-linear nature of this relationship, which implies r increases with F . To
387 propagate uncertainty in the estimates of b and d into the estimate of r we sampled the distributions
388 of b and d estimates to derive the distribution of r (SI Appendix, Text S4). Time to recovery from a
389 given level of depletion D to a defined proportion ϕ of K at which recovery is deemed to have
390 occurred (e.g. 0.95) was derived from the approach of Lambert et al. (22) (SI Appendix, Text S5).
391 When reporting recovery times, we report recovery from $0.5K$ to $0.95K$.

392

393 **Variables that determine the effect of trawling in comparative studies**

394 The effect of trawling on seabed biota in comparative studies could be influenced by different
395 variables. Thus we evaluated the explanatory power of several potential factors by including them as
396 covariates in a linear mixed model (39) based on equation (2) and selecting the most parsimonious
397 model using AIC. According to equation (2) the community response to trawling in \log_{10} scale is
398 approximately proportional to F , with slope a function of the ratio of d/r . The fixed part of the mixed
399 models was therefore:

400

$$401 \quad \log_{10}(\text{Response}) \sim \text{Trawling frequency} + \text{Trawling frequency} \times \text{other variables} \quad (4)$$

402

where the response variable is community biomass or numbers and where the ‘other variables’ can be covariates for d , r or their ratio. The intercept was removed because $\log_{10}(B/K)$ with no impact = 0. We modelled ‘study’ as a random effect, allowing the slope to vary per study. This approach accounted for the non-independence of observations within a study. We checked the assumptions of the linear mixed model by visual inspection of the normalized residuals (38).

We expected that factors that lead to a higher d would strengthen the effect of trawling (e.g. higher penetration depth), while factors that lead to a higher r by affecting growth rates of individuals and populations (higher flow of energy to the seabed because of a higher production or shallower depth, or a higher temperature) would weaken the effect. The closely related penetration depth P (continuous) and gear type (categorical) were examined as covariates for d . The following covariates for r were examined: primary production estimated from the vertically generalized productivity model ($\text{mg C m}^{-2} \text{ d}^{-1}$) (41) and particulate organic carbon flux to depth (POC flux, $\text{g C}_{\text{org}} \text{ m}^{-2} \text{ y}^{-1}$) (42) as proxies for energy availability, mean sea bottom temperature calculated from monthly mean bottom temperature for 2009-2011 provided in MyOcean Product; GLOBAL-REANALYSIS-PHYS-001-009, depth (from GEBCO if not reported in the original study), habitat type and sediment composition (gravel, sand and mud content). Habitat types were classified as biogenic habitats, gravel, sand, muddy sand/sandy mud, and mud. Sediment gravel, sand and mud content were extracted from the source studies by converting the sediment description to the Folk classification (43) and then converting the Folk classification to percentages based on the means in each category. In addition to analyses using covariates of d or r , we also conducted analyses using covariates of the d/r ratio, here the d/r ratio was approximated as the ratio of d or P to the continuous r covariates. The effect of trawling is expected to increase with water depth owing to the lower levels of natural disturbance in deeper water and the corresponding increase in the relative abundance of individuals

with slower life histories (low r), so $d \times \text{depth}$ was examined as a covariate for d/r , with depth expressed as a negative number.

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References

1. Halpern BS, et al. (2008) A Global Map of Human Impact on Marine Ecosystems. *Science* 319:948-952
2. Foden J, Rogers SI, Jones AP (2011) Human pressures on UK seabed habitats: a cumulative impact assessment. *Mar Ecol Prog Ser* 428:33-47
3. FAO (2016) The State of World Fisheries and Aquaculture 2016, FAO, Rome
4. Rice J (2005) Challenges, objectives, and sustainability: benthic community, habitats and management decision-making. *American Fisheries Society Symposium* 41:41-58
5. Rice J, et al. (2012) Indicators for Sea-floor Integrity under the European Marine Strategy Framework Directive. *Ecol Indic* 12:174-184
6. Rijnsdorp AD, et al. (2016) Towards a framework for the quantitative assessment of trawling impact on the seabed and benthic ecosystem. *ICES J Mar Sci* 73:S1: i127-i138
7. Eigaard OR, et al. (2016) The footprint of bottom trawling in European waters: distribution, intensity and seabed integrity. *ICES J Mar Sci* 10.1093/icesjms/fsw194
8. Gray JS, Dayton P, Thrush S, Kaiser MJ (2006) On effects of trawling, benthos and sampling design. *Mar Pollut Bull* 52:840-843
9. Sainsbury JC (1986) Commercial fishing methods. Fishing News Books, Oxford

10. Churchill JH (1989) The effect of commercial trawling on sediment resuspension and transport over the Middle Atlantic Bight continental shelf. *Cont Shelf Res* 9:841-864.
11. O'Neill F, Ivanović A (2016) The physical impact of towed demersal fishing gears on soft sediments. *ICES Journal of Marine Science: Journal du Conseil* 73-S1: i5-i14
12. Peterson CH, Summerson HC, Fegley SR (1987) Ecological consequences of mechanical harvesting of clams. *Fish Bull* 85:281-298
13. Collie JS, Escanero GA, Valentine PC (1997) Effects of bottom fishing on the benthic megafauna of Georges bank. *Mar Ecol Prog Ser* 155:159-172
14. Collie JS, Hermesen JM, Valentine PC, Almeida FP (2005) Effects of fishing on gravel habitats: assessment and recovery of benthic megafauna on Georges Bank. In: Barnes P, Thomas J (eds) *Benthic habitats and the effects of fishing*, Vol 41. American Fisheries Society, Bethesda, MD., p 325-343
15. Collie JS, Hall SJ, Kaiser MJ, Poiner IR (2000) A quantitative analysis of fishing impacts on shelf-sea benthos. *J Anim Ecol* 69:785-798
16. Kaiser MJ, et al. (2006) Global analysis and prediction of the response of benthic biota to fishing. *Mar Ecol Prog Ser* 311:1-14
17. van Denderen PD, et al. (2015) Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. *Mar Ecol Prog Ser* 541:31–43
18. Ramsay K, Kaiser MJ, Moore PG, Hughes RN (1997) Consumption of fisheries discards by benthic scavengers: utilization of energy subsidies in different marine habitats. *J Anim Ecol* 66:884-896
19. Duplisea DE, Jennings S, Warr KJ, Dinmore TA (2002) A size-based model of the impacts of bottom trawling on benthic community structure. *Can J Fish Aquat Sci* 59:1785-1795
20. Hiddink JG, et al. (2016) Bottom trawling affects fish condition through changes in the ratio of prey availability to density of competitors. *J Appl Ecol* 53:1500–1510
21. Rijnsdorp AD, Buys AM, Storbeck F, Visser EG (1998) Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. *ICES J Mar Sci* 55:403-419
22. Lambert GI, et al. (2014) Quantifying recovery rates and resilience of seabed habitats impacted by bottom fishing. *J Appl Ecol* 51:1326–1336
23. Ellis N, Pantus F, Pitcher CR (2014) Scaling up experimental trawl impact results to fishery management scales—a modelling approach for a “hot time”. *Can J Fish Aquat Sci* 71:733-746
24. Hiddink JG, Jennings S, Kaiser MJ (2006) Indicators of the Ecological Impact of Bottom-Trawl Disturbance on Seabed Communities. *Ecosystems* 9:1190–1199
25. Schaefer MB (1954) Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. *Inter-American Tropical Tuna Commission Bulletin* 1:23-56
26. McClanahan TR, Graham NA, Calnan JM, MacNeil MA (2007) Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. *Ecol Appl* 17:1055-1067
27. Costello C, et al. (2016) Global fishery prospects under contrasting management regimes. *Proceedings of the National Academy of Sciences*:201520420
28. Pitcher CR, et al. (2017) Estimating the sustainability of towed fishing-gear impacts on seabed habitats: a simple quantitative risk assessment method applicable to data-poor fisheries. *Methods Ecol Evol*
29. Hiddink JG, et al. (2006) Cumulative impacts of seabed trawl disturbance on benthic biomass, production and species richness in different habitats. *Can J Fish Aquat Sci* 63:721-736
30. Hughes KM, et al. (2014) Investigating the effects of mobile bottom fishing on benthic biota: a systematic review protocol. *Environmental Evidence* 3:23:DOI: 10.1186/2047-2382-1183-1123

31. Baird S, Wood BA, Bagley NW (2011) Nature and Extent of Commercial Fishing Effort on Or Near the Seafloor Within the New Zealand 200 N. Mile Exclusive Economic Zone, 1989-90 to 2004-05. Ministry of Fisheries, Wellington
32. Pitcher R, et al. (2016) Implications of current spatial management measures for AFMA ERAs for habitats. Report No. FRDC Project No 2014/204, CSIRO Oceans & Atmosphere, Brisbane
33. Bolam SG, et al. (2017) Differences in biological traits composition of benthic assemblages between unimpacted habitats. *Mar Environ Res*
34. Tillin HM, Hiddink JG, Kaiser MJ, Jennings S (2006) Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea basin scale. *Mar Ecol Prog Ser* 318:31-45
35. Brown CJ, Trebilco R (2014) Unintended cultivation, shifting baselines, and conflict between objectives for fisheries and conservation. *Conserv Biol* 28:677-688
36. Jennings S, Greenstreet SPR, Reynolds JD (1999) Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *J Anim Ecol* 68:617-627
37. Eigaard OR, et al. (2015) Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. *ICES J Mar Sci* 73 S1:i27-i43.
38. Zuur AF, et al. (2009) Mixed effects models and extensions in ecology with R. Springer Verlag, New York
39. Pinheiro J, Bates D, DebRoy S, Sarkar D (2013) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-113.
40. Jennings S, Lee J, Hiddink JG (2012) Assessing fishery footprints and the tradeoffs between landings value, habitat sensitivity and fishing impacts to inform marine spatial planning and an ecosystem approach. *ICES J Mar Sci* 69:1053-1063
41. Behrenfeld MJ, Falkowski PG (1997) Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnol Oceanogr* 42:1-20
42. Lutz MJ, Caldeira K, Dunbar RB, Behrenfeld MJ (2007) Seasonal rhythms of net primary production and particulate organic carbon flux to depth describe the efficiency of biological pump in the global ocean. *J Geophys Res Oceans* 112:C10011
43. Folk RL (1954) The distinction between grain size and mineral composition in sedimentary-rock nomenclature. *J Geol* 62:344-359

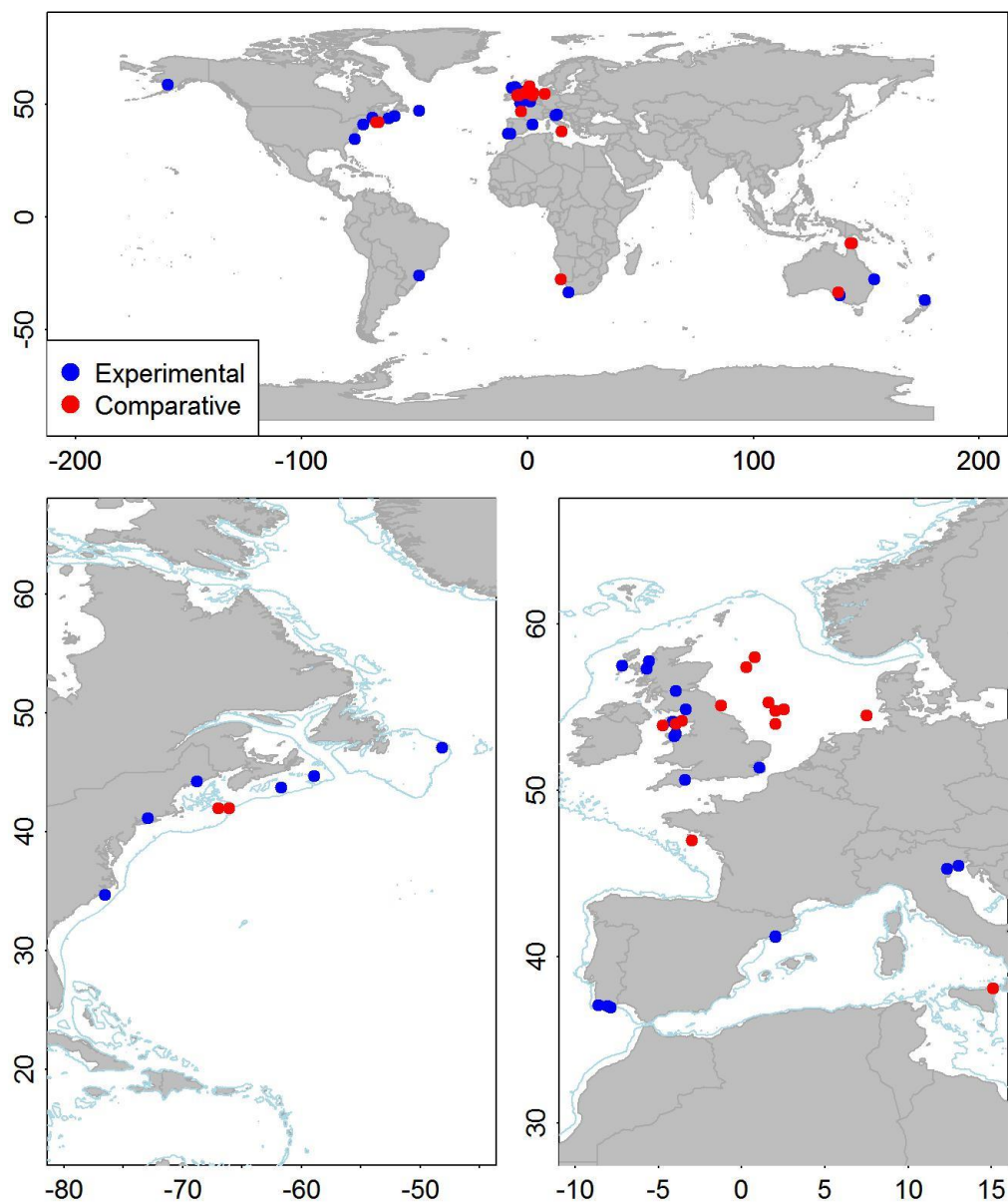
Table 1. Linear mixed model (SI Appendix, equation S3.1) fits for the analysis of data from comparative studies of changes in (A) biomass and (B) numbers. For community biomass the model with the lowest AIC included no explanatory variables other than trawling frequency, but for community abundance both 'Gravel content' and 'd/PP' improved the AIC in relation to a model without other explanatory variables. Results for these variables are given under (A) for comparative purposes.

A) Community biomass	Slope (<i>b</i>)	Std.Error	DF	t-value	p-value	AIC
TF	-0.07522	0.0158	503	-4.732	<0.0001	566.9
TF	-0.07142	0.0172	502	-4.148	<0.0001	568.4
TF: Gravel	-0.00067	0.0010	502	-0.648	0.5168	
TF	-0.08623	0.0325	502	-2.653	0.0082	568.8
TF : (<i>d</i> /PP)	125.6879	373.7966	502	0.336	0.7368	
B) Community numbers						
TF	-0.21185	0.1342	141	-1.577	0.1169	89.5
TF	-0.01451	0.0942	140	-0.153	0.8778	81.1
TF: Gravel content	-0.01206	0.0035	140	-3.377	0.0009	
TF	0.25300	0.2145	140	1.048	0.2964	86.1
TF: (<i>d</i> /PP)	-6892.96900	2676.5453	140	-2.575	0.0111	

TF = Trawling frequency *d* = depletion estimate from experimental studies (fraction per trawl pass, SI Appendix, Table S4), PP = Primary production (mg C m⁻² d⁻¹), Gravel = sediment composition in % by weight

554

555 **Figure captions**



556

557 Figure 1. Maps of the locations of the studies. The higher resolution maps of the northwest and
558 northeast Atlantic give more detail for two areas with high concentration of studies. The 200 m
559 depth contour is shown in blue.

560

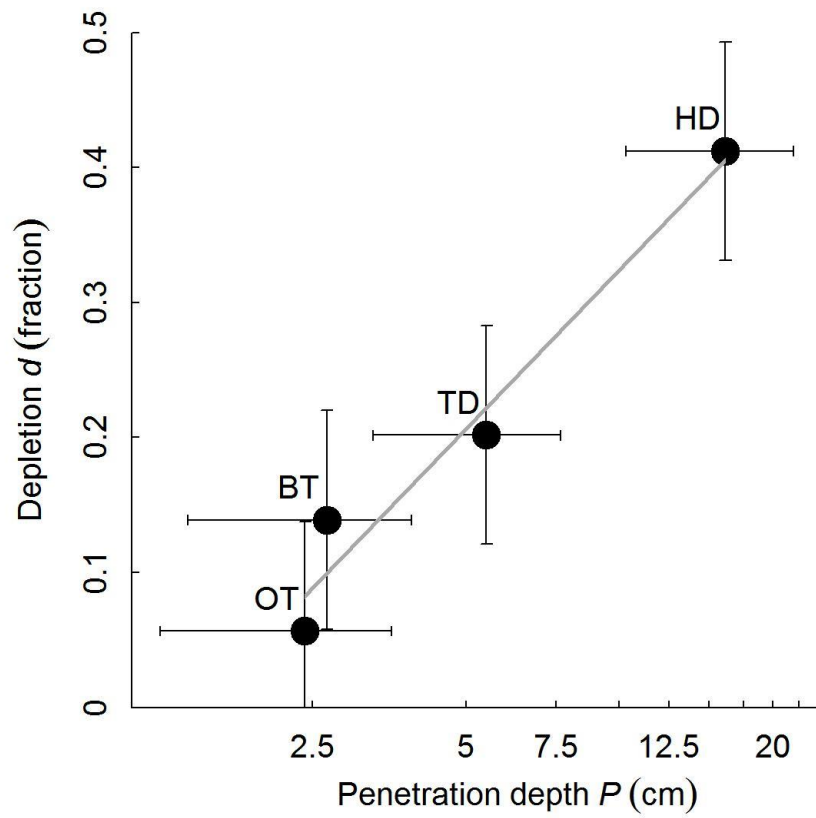


Figure 2. The relationship between the penetration depth P and depletion d of macrofaunal community biomass and numbers caused by a single trawl pass for different trawl gears. Means \pm SD.

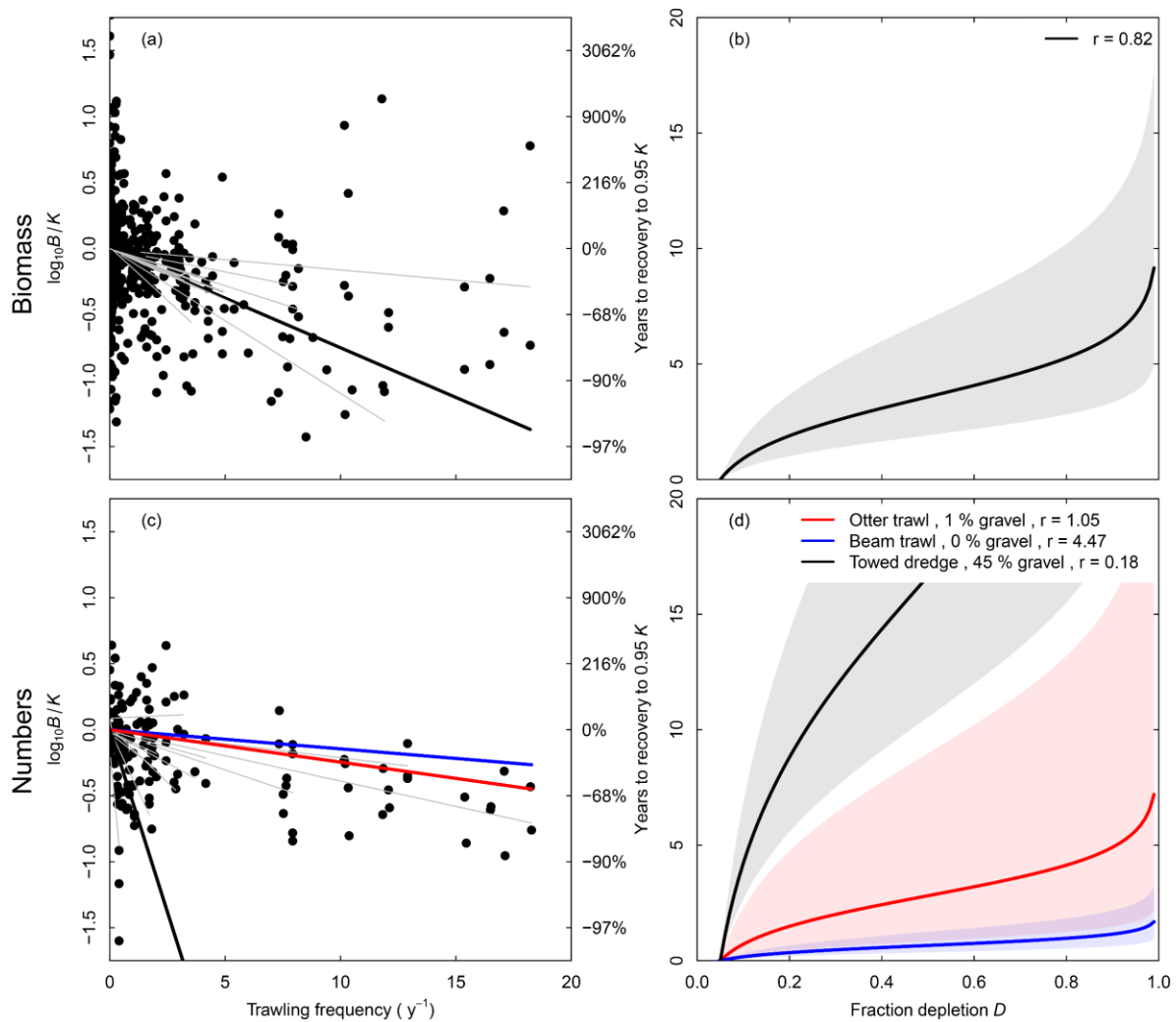


Figure 3. The relationship between trawling frequency and total community biomass (a) and numbers (c). The thicker lines are the fixed effects, grey lines the random effects of the individual studies (not all visible because many studies had small ranges and low trawling frequencies). Recovery time to 0.95K for depleted total community biomass (b) and numerical abundance (d) as a function of estimated r and initial depletion D . In (a) and (b) lines are the median estimate based on the mean d across all gears. In (c) and (d), lines are the median estimates for the three different gear types, based on the mean gravel content in the areas where studies using these gear types were carried out. The shaded areas indicate the 5–95% uncertainty intervals for estimates.